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Pointing the Way: The Distribution and Evolution of Some Characters of the Finger Muscles of Frogs

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ABSTRACT

The mm. transversi I and II of the hands of frogs have apparently shifted during the course of history from positions dorsal to the mm. flexores teretes III and IV to ventral positions—in the ancestor of Pipidae; and in the ancestor of a clade in Neobatrachia comprising *Allophryne ruthveni*, Brachycephalidae, Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, Pseudidae, Ranoidea, and *Rhinoderma darwini*, and excluding *Heleophryne*, Myobatrachidae, and Sooglossidae. Unique conditions of the m. transversus–m. flexor teres complex characterize Centrolenidae, Microhylidae, and a group of ranid frogs. The superficial flexors of the third finger are consistent in many families, but vary more than the deep muscles. There is an overall trend toward movement of the origins of the flexors from the palmar aponeurosis to the carpals. A hitherto undescribed muscle, the m. lumbricalis longus digiti III, occurs in *Batrachophrynus*, Calyptocephalellini, Heleophrynidae, *Lynchophrys*, and *Petropedetes*. Shared conditions in the superficial flexors support the monophyly of Myobatrachidae, hylodine origin of the Dendrobatidae, and placement of *Batrachophrynus* and *Lynchophrys* in Calyptocephalellini.

INTRODUCTION

The paucity of our knowledge of the evolution of frogs is reflected in the polytomies that predominate in the phylogenetic taxonomy presented by Ford and Cannatella (1993). These ambiguities indicate the need for new characters that can be used to resolve the uncertain relationships that now exist.

Hand muscles may seem unlikely to yield such characters, because the hands are in direct contact with the environment, so the muscles may be expected to be specialized for particular lifestyles, and hence subject to much convergence. Thus it seems reasonable to assume, for example, that the hand mus-

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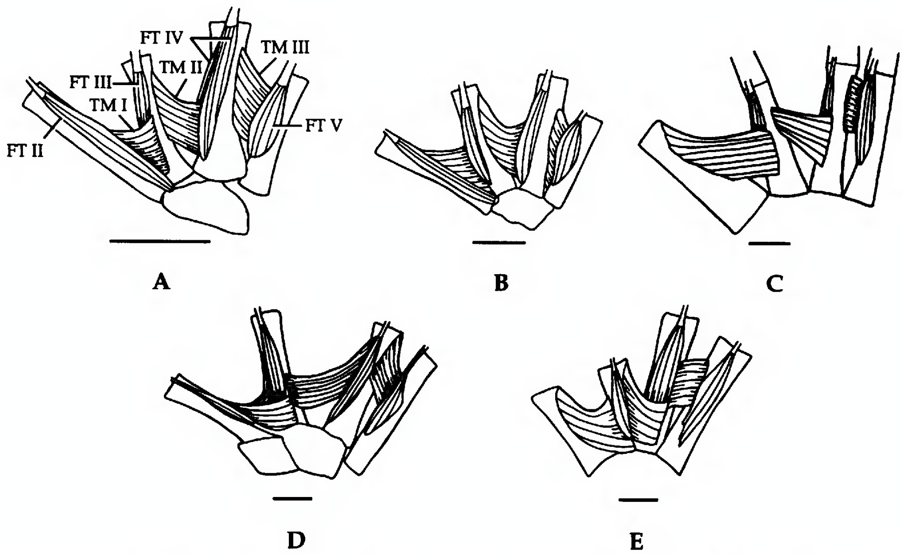

Fig. 1. Relationships between the mm. flexores teretes and the mm. transversi of the left hands of frogs, ventral view. **A.** *Rana sylvatica* UMMZ 138685(02174); **B.** *Limnodynastes dumerili* UMMZ 83395; **C.** *Bufo americanus* AMNH A78324; **D.** *Hylophorbus rufescens* AMNH A113450; **E.** *Hyalinobatrachium eurygnathum* AMNH A104094. In C and E, the m. flexor teres indicis is removed to reveal the insertion of the m. transversus metacarpi I. Abbreviations: FT II = m. flexor teres indicis II; FT III = m. flexor teres digiti III; FT IV = m. flexor teres digiti IV; FT V = m. flexor teres digiti V; TM I = m. transversus metacarpi I; TM II = m. transversus metacarpi II; TM III = m. transversus metacarpi III. Scale bars = 2 mm.

cles of arboreal frogs of any family will be similar, and that the different evolutionary histories of the different families will be obscured by the adaptive similarities. Burton (1996, 1998) demonstrated that the contrary was true: hand muscles show surprisingly few recognizable adaptations to lifestyle. Burton (1998) identified two sets of hand muscles whose distribution in Leptodactylidae and associated families suggested that they might be phylogenetically informative. In particular, Calyptocephalellini (*Caudiverbera* and *Telmatobufo*) possesses characters suggesting that it probably has a closer affinity to Heleophrynidae than to other Leptodactylidae.

Among the deepest muscles of a frog's hand are the mm. transversi metacarporum and the mm. flexores teretes. The mm. transversi are flat sheets of muscle that pass between the metacarpals of adjacent digits. Since there are four metacarpals, there are three mm. transversi. The m. transversus metacarpi I passes between Digits II and III; m. transversus II between Digits III and IV; and m. transversus III between Digits IV and V (fig. 1A). Contraction of the mm. transversi adducts the fingers, but depending on the positions of insertion of a m. transversus on the adjacent metacarpals, the palm may be closed (if the insertions are ventral on the metacarpals), opened (if they are dorsal), or rotated (if one insertion is dorsal and the other ventral).

The deepest flexor muscle of each finger is the m. flexor teres. This is always a slender muscle (the Latin word "teres" means "narrow"); usually it arises from the ventral or medial surface of the metacarpal, and inserts on the basal phalanx of the same digit. Contraction of a m. flexor teres bends the finger at the joint it crosses.

In some frogs, for example in myobatrachids (Egan, 1995), the attachments of the mm. transversi are relatively dorsal (fig. 1B). In these frogs the mm. flexores teretes digitorum III and IV arise from the ventral surface of the metacarpal, and lie ventral to the mm.

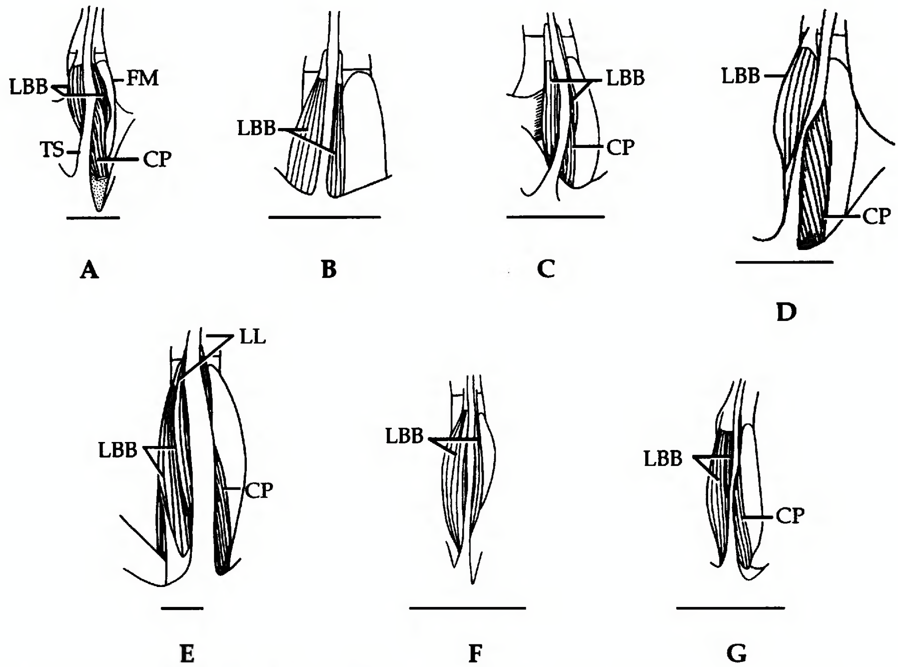

Fig. 2. Flexor muscles of third finger of left hands of frogs. **A.** *Bufo americanus* AMNH A124634; **B.** *Ascaphus truei* UMMZ 133050 (7392); **C.** *Scaphiopus hurteri* UMMZ 107147 (6445); **D.** *Limnodynastes dumerili* AMNH A59128; **E.** *Caudiverbera caudiverbera* UMMZ 56620; **F.** *Aromobates nocturnus* AMNH A130036; **G.** *Mantidactylus curtis* UMMZ 212708. CP = caput profundum; LBB = m. lumbricalis brevis digiti III; LL = m. lumbricalus longus digiti III; FM = m. flexor ossis metacarpi III; TS = tendo superficialis digiti III. Scale bars = 2 mm, except in B scale bar = 1 mm.

transversi metacarporum III and IV. In other frogs, for example in pelodryadines (Burton, 1996), the attachments of the mm. transversi are relatively ventral (fig. 1C). In these frogs, the origins of the mm. flexores teretes digitorum III and IV arise from more medially on the metacarpal, and lie dorsally to the mm. transversi. The mm. flexores teretes digitorum II and V always lie ventral to the adjacent mm. transversi. Egan (1995) and Burton (1996, 1998) demonstrated that these relationships between the muscles vary little within families.

The more superficial flexors of the third finger consist of a flexor tendon, the tendo superficialis digiti III, which passes from the distal edge of the palmar aponeurosis, and inserts upon the ventral surface of the ultimate phalanx (fig. 2A). This tendon is usually associated with a caput profundum, which arises from the carpals, and inserts on the dorsal side of the tendon. The m. lumbricalis brevis digiti III arises from the aponeurosis, or from the dorsal side of the tendon, or from the carpals, and inserts on the basal phalanx via a short tendon. Again, Egan (1995) and Burton (1996, 1998) reported little variation within families.

To test the potential of these sets of muscles as characters for use in phylogenetic analyses, I surveyed their relationships across all families of frogs.

MATERIALS AND METHODS

I examined the mm. flexores teretes III and IV and the mm. transversi metacarporum I and II in specimens of 378 species representing 183 genera from all of the living frog taxa represented in the phylogeny of Ford and Cannatella (1993). In many species, the deep muscles were exposed in the course of a dissection of the entire hand musculature, but in most species the muscles were ex-

posed by cutting through the skin along the metacarpals, and pushing the overlying muscles aside with fine forceps. The species used in this study are listed in appendix 1.

I also examined the superficial flexor musculature of the third finger of 337 species representing 159 genera of frogs from all of the living families. I exposed the musculature either in the course of a total dissection, or by a single incision in the skin, from the flexor surface of the wrist, and along the third finger to a point beyond the metacarpo-phalangeal joint. The skin was then held back by forceps to expose the muscles. In some specimens, the muscles were then cut, and pulled back to reveal their attachments; but in most specimens, I pushed and lifted muscle slips with forceps to find the attachments. The specimens examined are listed in appendix 1.

As salamanders are the most appropriate outgroup to use in comparisons with frogs, I examined the hand muscles of a number of caudates, and the figures and description of *Salamandra salamandra* of Francis (1934) (figures redrawn in Duellman and Trueb, 1986). Because the anatomical nomenclatures of salamanders and frogs have been derived independently, muscles that are identical in appearance and function, and are presumably homologous, bear different names. In describing the muscles of frogs, I use the nomenclature of Gaupp (1896). I follow Fabrezi and Alberch (1996) in numbering the digits of the frog hand from II to V, and Shubin (1994) in numbering the salamander fingers from I to IV.

RESULTS

Salamander–Frog Comparison

The smallest flexor of each finger of a salamander, the m. flexor digiti minimus, is a slender muscle that arises pennately from the metacarpal, and inserts via a short tendon on the basal phalanx. I assume that this muscle corresponds to the m. flexor teres of frogs. Between each pair of salamander metacarpals lies a flat muscle, the m. intermetacarpalis. I assume that this muscle corresponds to the m. transversus metacarpi of frogs.

The tendones superficiales of frogs correspond to the tendons of insertion of the m. flexor primordialis communis of salamanders. The only muscle in salamanders that corresponds with the mm. lumbricales longi of frogs is the m. flexor accessorius lateralis of the third finger of salamanders; this muscle corresponds to the m. lumbricalis longus digiti IV. If these muscles are homologous, then the absence of the m. lumbricalis longus digiti III appears to be the primitive condition in frogs. The mm. flexores breves superficiales of salamanders appear to correspond to the mm. lumbricales breves of frogs. In all of the salamanders examined, the mm. flexores breves arise from the tendo and adjacent aponeurosis; this appears to be the primitive condition in frogs.

Deep Musculature

The relative positions of the origins of the mm. flexores teretes and mm. transversi are consistent within families (table 1), except in the following cases.

In Leptodactylidae, the mm. flexores teretes are dorsal to the mm. transversi metacarporum except in Calyptocephalellini and *Eupsophus* (Burton, 1998). This variation is recorded as "dorsal or ventral" in table 1.

In Ranidae, the m. flexor teres digiti IV lies dorsal to the m. transversus metacarpi II, but, in addition, the following genera possess an extra slip of the m. flexor teres, which is ventral to the m. transversus—*Altirana*, *Aubria*, *Ceratobatrachus*, *Conraua*, *Hildebrandtia*, *Mantella*, *Mantidactylus*, *Petropedetes*, *Ptychadena*, *Pyxicephalus*, and *Rana* (fig. 1C). In table 1, I record taxa with the single slip as Ranidae (a), the taxa with two slips as Ranidae (b), "dorsal + ventral."

In Microhylidae (fig. 1D), the m. transversus metacarpi I usually consists of two slips, one slip passing between the distal ends of the metacarpals of Digits II and III, and a more proximal slip that arises proximally on the metacarpal of Digit III, and inserts on the metacarpus of Digit II just proximal to the other slip. Thus, I now interpret the unnamed muscle "M" of Burton (1983a, 1983b) as a slip of the m. transversus metacarpi I. In most species, the m. flexor teres digiti III passes dorsally to the proximal slip of the m. transversus, and ventrally to the distal slip. In table 1, I record this condition as "dorsal/ventral." The m. tranversus metacarpi II of

TABLE 1
Positions of the Origins of the Mm. Flexores Teretes III and IV Relative to the Corresponding Mm. Transversi Metacarporum I and II

Taxon	m. flexor teres III	m flexor teres IV
Caudata	ventral	ventral
Ascaphus truei	ventral	ventral
Leiopelma	ventral	ventral
Bombinatoridae	ventral	ventral
Discoglossidae	ventral	ventral
Megophryidae	ventral	ventral
Pelobatidae	ventral	ventral
Pelodytes	ventral	ventral
Rhinophrynus dorsalis	ventral	ventral
Pipidae	dorsal	dorsal
Limnodynastinae	ventral	ventral
Myobatrachinae	ventral	ventral
Sooglossidae	ventral	ventral
Heleophryne	ventral	ventral
Leptodactylidae	dorsal or ventral	dorsal or ventral
Bufonidae	dorsal or ventral	dorsal or ventral
Allophryne ruthveni	dorsal	dorsal
Brachycephalidae	dorsal	dorsal
Rhinoderma	dorsal	dorsal
Hylidae	dorsal	dorsal
Pseudidae	dorsal	dorsal
Centrolenidae	ventral	dorsal
Microhylidae	dorsal/ventral	ventral
Dendrobatidae	dorsal	dorsal
Hemisus	dorsal	dorsal
Arthroleptidae	dorsal	dorsal
Ranidae (a)	dorsal	dorsal
Ranidae (b)	dorsal	dorsal + ventral
Hyperoliidae	dorsal	dorsal
Rhacophoridae	dorsal	dorsal

Note: "dorsal/ventral" = the m. flexor teres passes between two slips of the m. transversus; "dorsal or ventral" = in some species the m. flexor teres is dorsal to the m. transversus, but in others it is ventral; "dorsal + ventral" = there are two slips of the m. flexor teres, one dorsal to the m. transversus, the other ventral.

microhylids is unusual also. Its connection to the second metacarpal lies proximally on the ventral surface, but the connection to the third metacarpal is very distal and on the medial surface (fig. 1D). The m. flexor teres digiti III is lacking in *Breviceps*, and in *Platypelis*, which also lacks the m. flexor teres digiti IV, and the distal slip of the m. transversus metacarpi I is absent in *Oreophryne*. I omit these genera from table 1.

In Bufonidae, the mm. flexores teretes lie dorsal to the mm. transversi in all species, except for *Ansonia, Nectophryne*, and *Oreophrynella*, in which the mm. flexores are ventral to the mm. transversi. This variation is recorded as "dorsal or ventral" in table 1.

Superficial Musculature of the Third Finger

Some frogs possess a superficial flexor muscle that has not previously been described. From the dorsal surface of the tendo arises a m. lumbricalis, in the form of a pair of slender slips that insert on the basal phalanx on both sides of the tendo. This muscle is identical in form to the m. lumbricalis longus digiti IV, except that it inserts on the basal phalanx. Digit IV contains three phalanges; Digit III contains two, thus in each case this m. lumbricalis inserts on the penultimate phalanx. I identify this muscle of Digit III as the m. lumbricalis longus digiti III. Andersen

(1978) figured and labeled a m. lumbricalis longus digiti III in a number of figures in his atlas, but claimed in the text that mm. lumbricales longi occur on only the fourth and fifth digits. The m. lumbricalis longus digiti III occurs in *Alytes, Batrachophrynus*, the Calyptocephalellini (fig. 2E), the Heleophrynidae, *Lynchophrys*, and *Petropedetes*.

In many species, a caput profundum arises from the carpals. Since the degree of fusion of the carpals varies between frogs, an attempt to identify the exact origin of the caput in each case would lead to unnecessary confusion, and give a false impression of variability. The caput always arises laterally to the tendo. In species that I have inspected, it originates from either the third carpal, or from fused bone that includes the third carpal.

The superficial flexors vary in the following characters: presence of caput profundum; presence of a m. lumbricalis longus digiti III; and the origin of the m. lumbricalis brevis digiti III, from the aponeurosis palmaris, the tendo superficialis, the carpals, or a combination of two of these. Little intraspecific variation was noted. Two of nine *Megaelosia goeldi* possess a small caput on one hand only, otherwise the caput is absent; the m. lumbricalis brevis digiti III arises in part from the carpals in *Astylosternus diadematus* (AMNH A23618). In *Kassina senegalensis* (AMNH A68535), and *Afrixalus osorioi* (AMNH A9425 and A9437), the m. lumbricalis brevis digiti III arises from the tendo superficialis as well as the carpals, whereas in other specimens it arises from the carpals alone. In *Ceratophrys cornuta* (KU 196428), *Limnodynastes dumerili* (UMMZ 83395), and *Heleophryne purcelli* (UMMZ 94139A and B), there is an additional slip from the aponeurosis to the medial side of this muscle. In most pelodryadines, the caput and tendo are sunken into the m. lumbricalis brevis to some degree, and in many species the latter is divided (Burton, 1996). Variation in this character occurs in *Litoria dahlii, L. ewingii, L. fallax, L. lesueuri, L. nannotis, L. peroni, L. thesaurensis, Nyctimystes humeralis*, and *N. pulchra*.

1. Presence of caput profundum

A. *Caput* absent—*Ascaphus* (fig 2A), *Bombina*, Dendrobatidae (fig. 2F), Discoglossidae, *Heleophryne natalensis, Hemisus, Hylodes asper, H. glaber, H. laterostrigatus, H. nasus, Hymenochirus, Leiopelma, Megaelosia, Pipa, Rhinophrynus*, Sooglossidae, *Zachaenus parvulus*.

B. Origin from carpals—other species.

2. Presence of m. lumbricalis longus digiti III

A. Present—*Batrachophrynus, Caudiverbera* (fig. 2E), *Heleophryne, Lynchophrys, Petropedetes, Telmatobufo*.

B. Absent—other species.

3. Origin of m. lumbricalis brevis digiti III

A. From tendo superficialis or adjacent aponeurosis only—*Ascaphus*(fig. 2B), Bombinatoridae, Discoglossidae, *Heleophryne, Hymenochirus, Leiopelma*, Myobatrachidae (fig. 2D), *Pipa, Rhinophrynus, Xenopus*.

B. Two origins: by narrow tendon from tendo superficialis or adjacent aponeurosis palmaris, and by tendon from carpals—*Batrachophrynus, Cardioglossus, Caudiverbera* (fig. 2E), *Discodeles*, Hyperoliidae (except *Kassina cochranae*), *Lynchophrys, Mantella baroni, M. femoralis, Mantidactylus* (fig. 2G), *Petropedetes, Phrynomerus, Platypelis, Plethodonthyla*, Rhacophoridae (except *Aglyptodactylus*), *Scotobleps, Telmatobufo, Trichobatrachus*.

C. From carpals only—other species.

Most families can be diagnosed by only one combination of characters. Variation occurs in Arthroleptidae, Leptodactylidae, Microhylidae, Pipidae, and Ranidae.

DISCUSSION

The relative positions of the mm. flexores and the corresponding mm. transversi appear to be very conservative characters, conflicting little with what is known of frog evolution. Although the superficial flexors vary more than the deep muscles, data from the superficial flexors may contribute to understanding of frog relationships. The caput profundum appears to have evolved in Mesobatrachia, possibly from a slip detached from the m. palmaris profundum. There appears to have been a trend for the origin of the m. lumbricalis brevis digiti III to migrate from the aponeurosis palmaris to the carpals. However, the mesobatrachian families Pelobatidae, Pelodytidae, and Megophryidae pos-

sess the condition prevalent in Neobatrachia, whereas the Myobatrachidae possess a condition more like that of Archaeobatrachia.

With caudates as the outgroup, the most parsimonious interpretation of the distribution of characters of the deep musculature is that the dorsal position of the mm. transversi relative to the mm. flexores teretes is the primitive condition in frogs. The ventral position appears to have evolved twice independently—in Pipimorpha, the ancestor of Pipidae, in which the hand is reversed for feeding; and once in Neobatrachia, in a common ancestor of the clade consisting of the following: *Allophryne ruthveni*; Brachycephalidae; Bufonidae; Leptodactylidae; the common ancestor of the Hylidae, Pseudidae, and Centrolenidae; *Rhinoderma*; and Ranoidea. To reduce repetition in the discussion to follow, I refer to this putative clade as "the advanced Neobatrachia." This same clade was identified, on the basis of position of amplexus, by Duellman and Trueb (1986), but Ford and Cannatella (1993) found the data relating to amplexus conflicting, and omitted this clade from their phylogeny.

By this interpretation, reversals may have occurred in Centrolenidae; Microhylidae; the bufonids *Ansonia, Nectophryne*, and *Oreophrynella*; and the leptodactylids *Caudiverbera, Eupsophus,* and *Telmatobufo*; or one or more of these taxa may be part of the sister group of the advanced Neobatrachia. Centrolenidae are probably part of the clade also containing Hylidae and Pseudidae (Ford and Cannatella, 1993), and, in that context, the ventral position of the m. flexor teres digiti III is a probable apomorphy of Centrolenidae. The unique conditions of the mm. transversi of Microhylidae are two more apomorphies of this family.

Whether the ventral positions of the mm. flexores teretes in the bufonids *Ansonia, Nectophryne,* and *Oreophrynella* represent the primitive condition of Bufonidae, or a reversal, is unclear. *Nectophryne afra* is a highly unusual bufonid. Noble and Jaeckle (1928) remarked on the striking similarity between the articular pads of *Nectophryne* and salamanders, and it is noteworthy that *Nectophryne* also displays a salamander-like condition of the deep hand musculature.

The mm. transversi of *Eupsophus* are so extensive that there is insufficient space to allow dorsal origins of the mm. flexores teretes (Burton, 1998). After examination of a wide range of frogs, I conclude that the broad mm. transversi of *Eupsophus* constitute a uniquely derived condition, with which the reversal of the mm. flexores teretes to the ventral positions is correlated.

The mm. transversi of Calyptocephalellini are not exceptionally developed, as in *Eupsophus*. Calyptocephalellini is "putatively the most primitive" tribe of the lower telmatobiines (Lynch, 1978). The possession of the primitive condition of the deep hand muscles by members of Calyptocephalellini may be further evidence of the primitiveness of this tribe, and evidence that they are the part of the sister group of the advanced Neobatrachia.

However, possession of the m. lumbricalis longus digiti III, which appears to be a derived condition, suggests a close relationship with *Batrachophrynus* and *Lynchophrys*. The most parsimonious of Lynch's (1978) trees identifies a clade consisting of Calyptocephalellini and *Batrachophrynus* (including the species that now constitutes *Lynchophrys*). The addition of this new character would increase the superiority of this tree over the next most parsimonious tree, on which Lynch based his taxonomy, in which *Batrachophrynus* was excluded from Calyptocephalellini. If the clade *Batrachophrynus* + Calyptocephalellini + *Lynchophrys* is accepted, the most parsimonious explanation of the ventral position of the mm. flexores teretes in Calyptocephalellini would be a reversal in their ancestor, since the alternative would require independent acquisition of the dorsal position by the ancestor of *Batrachophrynus* and *Lynchophrys*, and by the ancestor of the rest of the lower Telmatobiinae. On the basis of these additional data, I propose that *Batrachophrynus* and *Lynchophrys* be moved from Telmatobiini and placed in Calyptocephalellini.

The possession of two slips of the m. flexor teres digiti IV is a uniquely derived condition that arose within Ranidae, and is evidence of a unique common ancestry of the genera *Altirana, Aubria, Ceratobatrachus, Conraua, Hildebrandtia, Mantella, Mantidactylus, Petropedetes, Ptychadena, Pyxicephalus*, and *Rana*. Possession of this unique

character is in conflict with the characters on which the current subfamilial classification is based. In each of the ranoid families, some taxa possess the additional medial slip to the m. lumbricalis brevis digiti III, whereas other taxa lack the slip. The superficial flexors may present characters useful in determining relationships within these families, but exploration of these relationships lies beyond the scope of this paper.

The relationships of Dendrobatidae are controversial. Ford (1991) presented evidence that supports the hypotheses that the sister group of Dendrobatidae is either (1) Hylodinae or (2) a ranoid, and the presence of a ventral slip to the m. flexor teres digiti IV, as in some ranoids, would have given powerful support for the latter hypothesis. However, the occurrence of this slip varies within the ranoid subfamilies, so the absence of a ventral slip in Dendrobatidae refutes neither hypothesis. However, some support is given to a relationship between Hylodinae and Dendrobatidae from the superficial musculature, as the unusual condition of lacking any fibrous connection to the tendo superficialis or the adjacent aponeurosis is almost restricted to the hylodine genera *Hylodes* and *Megaelosia*, and Dendrobatidae. This condition is found also in *Hemisus, Zachaenus parvulus* (not *Z. stejnegeri*), and Sooglossidae.

The occurrence of the same rare combination of characters of the superficial flexors in all Limnodynastinae and Myobatrachinae is interesting, because there are no apomorphies to support the Myobatrachidae (Ford and Cannatella, 1993). The myobatrachid condition occurs elsewhere only in unrelated genera in variable taxa (*Asternostylus* and *Xenopus*).

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APPENDIX 1: SPECIMENS EXAMINED

The specimens examined are deposited in the following institutions: American Museum of Natural History (AMNH); Department of Zoology, University of Adelaide (AUZ); Department of Biology, East Tennessee State University (ETSU); Natural History Museum, University of Kansas (KU); National Museum of the Federal University of Rio de Janiero (MNUFRJ); Museum of Victoria, Australia (NMV), University of Michigan Museum of Zoology (UMMZ). Specimens marked "a" were used in the study of the superficial muscles of Digit III; specimens marked "b" were used in the study of both the superficial muscles of Digit III and the transversus—flexor teres system; unmarked specimens were used in the study of the transversus—flexor teres system only.

Caudata — *Aeneides lugubris* UMMZ 72635; *Ambystoma maculata* ETSUb; *A. mexicanum* ETSUb; *Dicamptodon ensatus* UMMZ 134829 (3746); *Hynobius nigrescens* UMMZ 131038; *Necturus maculosus* UMMZ 118845; *Siren lacertina* UMMZ 106373(3882). ***Anura*** — **Allophrynidae**: *Allophryne ruthveni* AMNH A139265b; KU 166730. **Arthroleptidae**: *Arthroleptis adelfifriederiei* AMNH A72759b; *A. poecilinotus* AMNH A3140; *A. stenodactylus* AMNH A12640b; *A. variabilis* KU 171792; *A. wahlbergi* AMNH A73374; *Astylosternus diadematus* AMNH A23618b; *Cardioglossus leucomystax* AMNH A9311a, AMNH A9312a, AMNH A9313b; *Leptodactylodon albiventris* AMNH A23609b; *Schouttedenella xenochirus* AMNH A73864; *S. xenodactyla* AMNH A68686a; *Scotobleps japonicus* AMNH A65671a; *Trichobatrachus robustus* AMNH A129866a. **Ascaphidae**: *Ascaphus truei* AMNH A20648a, AMNH A36532a, KU 153191, UMMZ 133050 (7392)b. **Bombinatoridae**: *Bombina bombina* AMNH 64934a: *B. orientalis* AMNH A58771, KU 38614; *B. variegata* AMNH A65114a, AMNH A72535; *Barbourula busuangensis* AMNH A57552. **Brachycephalidae**: *Brachycephalus ephippium* AMNH A77353, UMMZ (untagged)b, UMMZ 38256b. **Bufonidae**: *Ansonia longidigita* AMNH A22919b; *A. muelleri* AMNH A69963b; *Atelopus cruciger* AMNH A70794b; *A. ignascena* AMNH A17486b. AMNH A17493b; *Bufo americanus* AMNH A78324b, AMNH A124634b; *B. bufo* AMNH A134236b; *B. brauni* AMNH A70129b; *B. haematiticus* AMNH A54640b, AMNH A55493b, AMNH A89454b; *B. marinus* AMNH 101876b, AMNH A114843b; KU 181621b; *B. valliceps* AMNH A7018b, AMNH A89127b, AMNH A119666b; *B. woodhousei* AMNH A32417a; *Capensibufo rosei* AMNH A144948b; *Dendrophryniscus minutus* AMNH A114908, AMNH A114910b; *Melanophryniscus moreirae* AMNH A16998, AMNH A17029b, AMNH A74413; *M. stelzneri* AMNH A50645; *Nectophryne afra* AMNH A9451b; *Nectophrynoides tornieri* AMNH A72718b; *N. viviparus* AMNH A33213b; *Nimbaphrynoides liberiensis* AMNH A83261b; *Oreophrynella quelchii* AMNH A99620b, AMNH A9624b; *Pedostibes hosii* AMNH A23815b; *Peltophryne guentheri* KU 264090; *P. longinasus* AMNH A101828; *P. peltocephala* AMNH A61200, AMNH A61205a. **Centrolenidae**: *Centrole-*

ne buckleyi KU 178047, KU 178079; *C. geckoideum* KU 178015; *C. prosoblepon* UMMZ 117672 (7643)b, UMMZ 167399b; *Cochranella albomaculata* UMMZ 131878 (4440)b; *C. cochranae* UMMZ 92098b; *Hyalinobatrachium colymbiphyllum* KU 65238; *H. eurygnathum* AMNH A104094b; *H. fleischmanni* AMNH A51846a, UMMZ 131879b. **Dendrobatidae**: *Aromobates nocturnus* AMNH A130032–33, AMNH A130036–38b; *Colostethus inguinalis* AMNH (uncataloged skinned carcasses, 11 specimens)b; *C. olmonae* AMNH (uncataloged skinned carcasses, 12 specimens)b; *C. pratti* AMNH (uncataloged skinned carcasses, 12 specimens)a; *C. riveroi* KU 133049; *C. talamancae* AMNH (uncataloged skinned carcasses, 3 specimens)a; *C. trinitatius* AMNH (uncatalogued skinned carcasses, 12 specimens)b; *Dendrobates auratus* AMNH (uncataloged skinned carcasses, 10 specimens)b, KU 116994, KU 116997; *D. histrionicus* AMNH (uncataloged skinned carcasses, 12 specimens)a; *D. lehmanni* AMNH (uncataloged skinned carcasses, 10 specimens)b; *D. pumilio* AMNH (uncataloged skinned carcasses, 10 specimens)a; *D. speciosus* AMNH (uncataloged skinned carcasses, 11 specimens)b; *D. truncatus* (uncataloged skinned carcasses, 7 specimens)a; *Epipedobates espinosai* AMNH (uncataloged skinned carcasses, 11 specimens)a; *E. pictus* AMNH (uncataloged skinned carcasses, 5 specimens)a; *E. tricolor* AMNH (uncataloged skinned carcasses, 10 specimens)a; *E. trivittatus* KU 172042; *Minyobates mimulus* AMNH (uncataloged skinned carcasses, 10 specimens)a; *M. steyermarki* (AMNH (uncataloged skinned carcasses, 11 specimens)a; *Phyllobates aurotaeniata* AMNH (uncataloged skinned carcasses, 10 specimens)a; *P. lugubris* AMNH (uncataloged skinned carcasses, 10 specimens)b; *P. vittatus* AMNH (uncataloged skinned carcasses, 10 specimens)b. **Discoglossidae**: *Alytes muletensis* AMNH A146044b; *A. obstetricans* AMNH A41326b, AMNH A145205a, KU 14185; *Discoglossus pictus* AMNH A50715a, AMNH A51167b; *D. sardus* AMNH A652b. **Heleophrynidae**: *Heleophryne natalensis* AMNH A74139b; KU 105925b; *H. purcelli* UMMZ 94139b (2 specimens). **Hemisotidae**: *Hemisus guttatus* KU 195800; *H. marmoratus* AMNH A73892a, AMNH A83269a; *H. olivacea* AMNH A8935a. **Hylidae**: *Acris crepitans* UMMZ 68992 (2 specimens)b; *A. gryllus* AMNH A122741a; *Agalychnis moreleti* AMNH A 13822b; *Cyclorana australis* AM R97535b, AM R97533b, SAM SAM R25775b; *C. cryptotis* AUZb; *C. cultripes* AUZb; *C. longipes* AUZb; *C. maini* SAM R20288b, SAM R20291b; *C. novaehollandiae* AM R143850b; *C. platycephala* AUZb, SAM R27358b, SAM R45747b; *C. vagitus* AUZ; *Duellmanohyla uranochroa* AMNH A114595a; *Gastrotheca pseustes* KU 178491; *Hemiphractus johnsoni* AMNH A42862a; *H. proboscideus* KU 123158; *Hyla pellucens* KU 178742; *H. vasta* AMNH A23141b; *Hyla versicolor* SAM R10063, 11562; *Litoria alboguttata* SAM 11831b, SAM R34993b; *L. angiana* AM R21681b, AM R21690b, AM R21690b, AM R21692b, AM R21695b; *L. arfkiana* AM R114685b, AM R114689b; *L. aurea* AM R74546b, AM R74550b; *L. bicolor* AUZb; *L. booroolongensis* AM R34442b; *L. castanea* AM R32567b, AM R32576b, AM R32583b; *L. chloris* SAM R12268b, SAM R25760b; *L. citropa* AM R76622b; *L. coplandi* AM R140176b, AM R140177b; *L. dahlii* AM R97394b, AUZb; *L. darlingtoni* AM R18064b; *L. dentata* AM R78930b, AUZb; *L. eucnemis* (= *L. serrata*) AM R26804b; *L. ewingi* AUZb, SAM R34903b; *L. fallax* AUZ (2 specimens)b; *L. freycineti* AM R78914b, AM R78915b, AM R78916b, SAM R12186b, SAM R12190b; *L. gracilenta* AUZb; *L. inermis* AUZb; *L. infrafrenata* AUZb, SAM R34907b, SAM R34970b; *L. latopalmata* AUZb, SAM R19672b, SAM R19701b; *L. lesueuri* AUZb, SAM R35336b; *L. meiriana* SAM R9097b, SAM R19638b; *L. microbelos* SAM R25463b; *L. micromembrana* AM R119597b, AUZb; *L. modica* AM R132497b, AM R132498b, AUZb; *L. moorei* AM R140571b; *L. nannotis* AM R56415b, AM R56418b, SAM R12140b; *L. nasuta* SAM R43445b; *L. nyakalensis* AM R61394b, AM R61395b; *L. phyllochroa* AUZb, SAM R39011b; *L. pallida* AM R97375b, AM R97376b; *L. peroni* AUZb, SAM R25771b, SAM R43163b; *L. piperata* AM R36448b; *L. raniformis* SAM R13164b; *L. rheocola* AM R56528b; *L. rothii* AUZb;

L. rubella AM R88659b; *L. subglandulosa* AM R51739b; *L. thesaurensis* AM R121621b, AM R121629b; *L. tornieri* AUZb; *L. verrauxi* AUbZ; *L. wotjulumensis* AUZb; *L. xanthomera* AUZb; *Nyctimystes dayi* SAM R12304b; *N. daymani* AM R18026b; *N. disrupta* AM R21636b; *N. foricula* AM R22206, AM R22226b, AM R22229b; *N. humeralis* AM R132334b, AM R132335b; *N. kubori* AM R22311b; *N. pulchra* AM R140613b, AM R140622b; *Osteopilus dominicensis* AMNH A31261b; *O. taurinus* KU 175208; *Pachymedusa dacnicolor* KU 87138; *Pelodryas caerulea* SAM R33435b; *P. splendida* AUZb; *Phrynohyas venulosa* KU I71336; *Phyllomedusa burmeisteri* KU 92319; *P. sauvagii* AMNH A144518b; *Pseudacris brachyphona* KU 156154; *Pternohyla dentata* AMNH A107018; *P. fodiens* UMMZ 117350 (3569)b; *Scinax nasica* SAM R10522; *Triprion spatulata* AMNH A13840, UMMZ 104418b. **Hyperoliidae:** *Afrixalus osorioi* AMNH A9415, AMNH A9425a, AMNH A9428a, AMNH A9437a, AMNH A9442a; *Cryptothylax greshoffi* AMNH A63547b; *Heterixalus betsilio* AMNH A50429a, AMNH A50431; *Hyperolius cystocandicans* UMMZ 137253 (3 specimens)b; *H. kivuensis* AMNH A73295Bb AMNH A73296a; *H. marmoratus* AMNH A99740a, AMNH A99743a, AMNH A99744a; KU 195822; *H. viridiflavus* UMMZ 150122b; *Kassina cochranae* AMNH A83535b, AMNH A83546; *K. senegalensis* AMNH A68534, AMNH A68535b, AMNH A68537b; *Leptopelis bacagei* AMNH A74108b AMNH A74109a; *L. calcaratus* AMNH A59472; *L. christyi* KU 155139; *Phlyctimantis leonardi* AMNH A83569a, AMNH A83564a, *P. verrucosus* AMNH A8665; *Tachycnemis seychellensis* UMMZ 175476b. **Leiopelmatidae:** *Leiopelma hochstetteri* AMNH A51311b, AMNH A51314, UMMZ 177463a; **Leptodactylidae:** *Adenomera andreae* KU 149367b, KU 152401b; *Alsodes nodosus* AMNH A23944; *A. vanzolini* KU 160568b, KU 16220b8; *Atelognathus patagonicus* KU 160428b; *A. praebasalticus* KU 180991b; *A. reverberi* KU 180997b; *Barycholos pulcher* KU 142177b, KU 142187b, KU 142192b; *Batrachophrynus macrostomus* AMNH A6737, AMNH A6738, KU 173106b; *Batrachyla taeniata* KU 161482b, KU 161482b, KU 161483b; *Caudiverbera caudiverbera* AMNH A23915b, KU 159941b, KU 164189b, UMMZ 56620b; *Ceratophrys calcarata* KU 144966b, KU 207528b; *C. cornuta* KU 196428b, UMMZ 66529b; *C. ornata* KU 175560b; *Chalcophrys pierotti* KU 191928b; *Crossodactylus dispar* KU 92750b, KU 92751b; *C. gaudichaudi* KU 74190b; *C. sp.* AMNH A103788–91a; *Cyclorhampus asper* KU 71493b, KU 84715b, KU 92770b; *C. eleutherodactylus* KU 92781b; *C. fuliginosus* KU 92786b; *Dischidodactylus duidensis* AMNH A23194, AMNH A23195; *Edalorhina perezi* KU 177448b, KU 215452b; *Eleutherodactylus augusti* KU 39827b, KU 39832b, KU 39833b; *E. bransfordi* KU 113683b; *E. fitzingeri* KU 65870b, KU 172268b, KU 172278b; *E. fleischmanni* KU 30918b, KU 65837b, KU 65850b; *E. raniformis* KU 114529b, KU 114548b, KU 145003b; *E. achatinus* KU 165100b, KU 202280b, KU 202282b, KU 217824b; *E. coqui* KU 180639b; *E. martinicensis* KU 282501b, KU 282517b, KU 282544b; *E. octavioi* KU 92827b, KU 113684b; *E. phoxocephalus* KU 131427b, KU 166060b; *E. w-nigrum* KU 202560b, KU 202580b; *E. karlschmidti* KU 281335b; *E. schmidti* KU 286267b, KU 286268b, KU 286277b, KU 286280b; *E. inoptatus* KU 280115b, KU 280411b, KU 280413b, KU 280414b; *E. leprus* KU 137517b; *E. pipilans* KU 58905b, KU 58908b; *Eusophus migueli* KU 162234b; *E. roseus* KU 162151b; *E. vertebralis* KU 162237b; *Holoaden bradei* KU 92865b; *Hydrolaetare schmidti* KU 220360b; *Hylodes asper* AMNH A103830a, AMNH A103835–42a, KU 74214b, KU 92873b; *H. glaber* AMNH A103881a; *H. laterostrigatus* AMNH A103898a, AMNH A103903-8a, KU 92876b, KU 92880b; *H. nasus* AMNH A72456a; *H. ornatus* AMNH A103913a; *H. perplicatus* AMNH A15527a; *H. pulcher* AMNH A103927a, AMNH A103941–3a; *Hylorina sylvatica* KU 161391b; *Insuetophrynus acarpicus* KU 161414b; *Ischnocnema quixensis* KU 123245b; *Lepidobatrachus asper* KU 80782b; *L. llanensis* KU 128856b; *Leptodactylus fuscus* KU 115338b, KU 166429b, KU 166430b; *L. pentadactylus* KU 25713b, KU 35928b, KU 65715b, KU 65717b; *L. rhodomystax* KU 122581b; *L.*

rhodonotus KU 138883b, KU 205220b; *Limnomedusa macroglossa* KU 197270b; *Lithodytes lineatus* KU 207750b; *Lynchophrys brachydactylus* KU 139048b, UMMZ 68309b; *Megaelosia goeldi* AMNH A70249, AMNH A103947–53, KU 92963b; *Odontophrynus americanus* KU 100439b; *O. occidentalis* KU 160696b; *Paratelmatobius lutzi* KU 92977b, KU 92978b; *Phrynopus biligoniger* KU 72865b; *P. flavomaculata* KU 119738b; *P. parkeri* KU 181294b, KU 181348b; *P. peruvianus* KU 138938b; *Physalaemus petersi* KU 120286b; *P. pustulosus* KU 58916b, KU 65625b, KU 125037b; *Pleurodema brachyops* KU 104363b, KU 166659b, KU 166665b; *P. cinerea* KU 135599b; *P. marmorata* KU 135773b; *P. tucumana* KU 160828b; *Proceratophrys cristiceps* KU 220085b; *Somuncuria somuncuriensis* KU 180987b; *Telmatobius brevipes* KU 181491b; *T. culeus* KU 174962b; *T. marmorata* KU 162916b; *T. peruvianus* KU 162058b, KU 162064b; *T. schreiteri* KU 160884b; *T. truebae* KU 212454b, KU 280413b; *Telmatobufo bullocki* MCZ A78829b; *T. venustus* KU 159811b; *Thoropa miliaris* KU 74202b, KU 74203b, KU 92855b; *Vanzolinius discodactylus* KU 119307b, KU 149295b, KU 178270b; *Zachaenus parvulus* KU 93078b, KU 93081b, MCZ A64356b, UMMZ 127921 (38676–7)a; *Z. stejnegeri* MCZ A100258a. **Megophryidae:** *Megophrys boettgeri* AMNH A30323b, AMNH A30389; *M. montana* AMNH A2993; *M. monticola* UMMZ 83072b. **Microhylidae:** *Albericus variegatus* AMNH (untagged); *Aphantophryne pansa* AMNH A58131; *Breviceps adspersus* AMNH A12716; *B. gibbosus* AMNH A3053b; *B. poweri* AMNH A73850b; *Calluella yunnanensis* AMNH A5450a; *Callulops personatus* AMNH A78096b; *C. robustus* AMNH A72555; *C. stictogaster* AMNH A13339, KU 93707; *Cophixalus biroi* AMNH A78105, AMNH A78111; *C. ornatus* AMNH A65443; *C. riparius* AMNH A130402; *C. verrucosus* AMNH A113230b; *Copiula oxyrhina* AMNH A59895 AMNH A140627b; *Dermatonotus mulleri* AMNH A56111; *Dyscophus gueneti* AMNH A23935b; *Gastrophryne carolinensis* AMNH A113324a; *G. olivacea* AMNH AM62736; *Hamptophryne boliviana* AMNH A115780; *Hylophorbus rufescens* AMNH A78215, AMNH A113450; *Hypopachus barberi* KU190404; *Kaloula verrucosa* AMNH A5298; *Mantophryne lateralis* AMNH A76007; *Microhyla heymonsi* AMNH A28395; *M. ornata* AMNH A6727a; *Nelsonophryne aequitoriala* AMNH A17556; *Oreophryne anthonyi* AMNH A58038; *O. flava* AMNH A58152b; *O. idenburgensis* AMNH A49665; *O. sp.* AMNH A98149; *Phrynomantis annectens* AMNH A97899b; *P. bifasciata* AMNH A22343; *Phrynomerus bifasciatus* UMMZ 61377b; *Platypelis grandis* AMNH A22376, AMNH A23750b; *Plethodonthyla ocellata* AMNH A23839, AMNH A50407a; *Pseudohemisus obscurus* AMNH A50480; *Relictovomer pearsei* AMNH A69883b; *Scaphiophryne marmoratus* AMNH A133700b, AMNH A133701a; *Sphenophryne brevipes* AMNH A130533; *Uperodon systoma* AMNH A75125; *Xenobatrachus obesus* AMNH A78193. **Myobatrachidae:** *Adelotus brevis* AMNH A59096a; *Crinia georgiana* AMNH A62271b, AUZ; *C. riparia* AUZ; *C. signifera* AMNH A40298a; KU 186927; *Geocrinia victoriana* AMNH A67160b; *Heleioporus albopunctatus* AMNH A104689a; *Lechriodus melanopyga* AMNH A81226a; *Limnodynastes dumerili* AMNH A59128a, AMNH A59129a, AMNH A63395b; NMV 24848, KU 179927, UMMZ 83395b; *L. fletcheri* AUZ, KU186887; *L. tasmaniensis* KU 57062, KU 57067; *Mixophyes balbus* AUZ; *M. iteratus* KU179961; *M. schevilli* AMNH A19942a; *Notaden nichollsi* AMNH A87221a; *Pseudophryne bibroni* AMNH A111053a. **Pelobatidae:** *Leptobatrachium hasseltii* AMNH A90490; *Pelobates varaldi* AMNH A62934b; *Scaphiopus couchi* UMMZ 114279 (2829)b; *S. holbrooki* AMNH A38305b, AMNH A51747; *S. hurteri* KU 11329, UMMZ 107147 (6445); *S. intermontanus* AMNH A62652. **Pelodytidae:** *Pelodytes caucasicus* AMNH A108329a; KU 203791; *P. punctatus* UMMZ 111990b. **Pipidae:** *Hymenochirus boettgeri* AMNH A23962a, AMNH A65661a; *H. camerunensis* AMNH A65660; *Pipa arrabali* AMNH A52820a, AMNH A52831b; *Silurana tropicalis* AMNH A145948; *Xenopus laevis* AMNH A37567a; AMNH A37572a; AMNH A45054; *X. muel-*

leri AMNH A53852b. **Pseudidae:** *Lysapsus lamellus* AMNH A98150; *L. mantidactylus* KU 93212; *Pseudis paradoxa* AMNH A55685, AMNH A146264b, MNUFRJ 14049. **Ranidae:** *Altirana parkeri* AMNH A53178; *Aubria subsigillata* AMNH A129925; *Batrachylodes vertebralis* AMNH A71744b; *B. wolfi* AMNH A71777, AMNH A71779; *Cacosternum boettgeri* AMNH A72776a; *C. capense* AMNH A97904; *Ceratobatrachus guentheri* AMNH A84299b; *Conraua alleni* AMNH A83301; *Discodeles bufoniformis* AMNH A71851b; *D. guppyi* AMNH A64278b; *Hildebrandtia ornata* AMNH A10880a, AMNH A10881; *Mantella aurantina* AMNH A73447a, AMNH A133612a, AMNH A133621a, AMNH A133624a, AMNH A133628–30a, AMNH A133633a, AMNH A133635a, AMNH A133637a, AMNH A133639b; *M. baroni* AMNH A133657b, AMNH A133659–61b, AMNH A133663a, AMNH A133671a, AMNH A133675–8a, AMNH A136887a; *M. betsilio* AMNH A140567; *M. laevigata* AMNH A140561a, AMNH A140564a; *M. viridis* AMNH A133683b; *Mantidactylus albofrenatus* AMNH A23901a, AMNH A23904b; *M. curtis* UMMZ 212708b; *M. femoralis* AMNH A133690b; *M. guttulatus* AMNH A50359a; *M. luteus* AMNH A50251a; AMNH A50255; *M. pliciferus* AMNH A50504b; *Meristogenys jerboa* AMNH A90566a, KU 155607, KU 155609; *Micrixalus tenasserimensis* AMNH A97869; *Nannophrys ceylonensis* AMNH A77467b; *Nanorana pleskei* AMNH A48771b; *Natalobatrachus bonebergi* AMNH A73899b; *Nyctibatrachus deccanensis* AMNH A23827b; *Occidozyga cyanophlyctis* KU 200413; *O. laevis* AMNH A72679a, AMNH A102928, AMNH A102939; *Palmatorappia solomonis* AMNH A71866b; *Petropedetes natator* AMNH A84604b, AMNH A84615; *P. palmipes* AMNH A23936a; *Phrynobatrachus dendrobates* AMNH A9119; *P. graueri* AMNH A68760; *P. natalensis* AMNH A129776; *Platymantis boulengeri* AMNH A64252; *P. corrugatus* AMNH A68164; *P. guppyi* KU 98164; *P. papuensis* AMNH A59972; *P. solomonis* AMNH A69320; *Ptychadena aequiplicata* AMNH A41878; *P. anchietae* KU 196067; *P. mascariensis* AMNH A11143; *Pyxicephalus adspersus* KU 195804; *Rana areolata* KU 209979; *R. berlandieri* KU 195391; *R. sylvatica* UMMZ 138685 (02174); *Staurois natator* AMNH A136068; *Strongylopus grayi* AMNH A13558; *Tomopterna labrosa* AMNH A23752. **Rhacophoridae:** *Aglyptodactylus madagascariensis* AMNH A50349a, AMNH A50536b, UMMZ 213604b; *Boophis albilabris* UMMZ 201442b, UMMZ 201443b; *B. goudoti* AMNH A23916b; *B. luteus* AMNH A23896b; *B. periegetes* UMMZ 198707; *B. tephraeomystax* UMMZ 213947; *Buergeria buergeri* AMNH A53106, AMNH A112693; *B. japonicus* AMNH A82494b, AMNH A82496b; *Chirixalus doriae* AMNH A26758, AMNH A26771a; *Chiromantis rufescens* AMNH A9391b; *Polypedates dennysi* AMNH A30530b; *P. leucomystax* AMNH A30069, AMNH A68170; *P. megacephalus* UMMZ 182716b, UMMZ 189970b; *Rhacophorus maculata* KU 193643; *R. moltrechti* UMMZ 182217b, UMMZ 199814b, UMMZ 199849b; *R. oxycephalus* AMNH A26845b. **Rhinodermatidae:** *Rhinoderma darwini* AMNH 57314a; KU 161506, KU 161544. **Rhinophrynidae:** *Rhinophrynus dorsalis* AMNH A6214b, AMNH A6223a, AMNH A6226a, UMMZ 82134b. **Sooglossidae:** *Nesomantis thomasseti* UMMZ 145679b; *Sooglossus gardineri* UMMZ 23506b, UMMZ 183084b; *S. sechellensis* AMNH A26792b, UMMZ 150830b.